

BIODIVERSITY, SPECIES COMPOSITION AND DISTRIBUTION OF MARINE SPONGES IN NORTHEAST AUSTRALIA

JOHN N.A. HOOPER, JOHN A. KENNEDY, SUSAN E. LIST-ARMITAGE, STEPHEN D. COOK AND RON QUINN

Hooper, J.N.A., Kennedy, J.A., List-Armitage, S.E., Cook, S.D. & Quinn, R. 1999 06 30: Biodiversity, species composition and distribution of marine sponges in northeast Australia. *Memoirs of the Queensland Museum* 44: 263-274. Brisbane. ISSN 0079-8835.

Biodiversity, species composition and biogeographic relationships were compared between 18 regional populations of marine sponges along the NE Australian coastline (extending northwards from Byron Bay to the E Gulf of Carpentaria, including the southern fauna from Sydney-Illawarra as an outgroup comparison), based exclusively on samples of living populations. Much of the older literature concerning Australian sponge taxonomy is too unreliable to be used effectively as a tool to determine conspecificity and explore faunistic relationships, and consequently this literature was ignored completely in our analyses using instead recent collections made throughout the study area, all documented in situ.

Levels of biodiversity varied considerably between many regions, related in part to the size and diversity of habitats present in particular regions, but also to differences in collection effort. Several regions with apparently low sponge diversity (e.g. 3 seamounts in the Coral Sea) were clearly biased by correspondingly low collection efforts, whereas in other regions these biodiversity data appear to be more realistic indicators of species richness. Faunas of the Gulf of Carpentaria and Turtle Islands were more intensively sampled but had relatively low sponge diversity, whereas those of the Swain Reefs, Capricorn-Bunker Group, Lizard Island and Moreton Bay regions had much higher species diversity with equivalent (and sometimes lower) collection effort. Five of the seven relatively highly diverse regions lay in the south (Swain Reefs, Capricorn-Bunker Group, Moreton Bay, Sydney-Illawarra, Sunshine Coast), with only two northern regions showing comparable diversity (Lizard Island, Low Isles), contrary to latitudinal trends in diversity found in some other marine phyla. Statistically these trends do not appear to be artifacts of sampling effort but reflect true differences in provincial diversity.

The number of unique (apparent endemic) species within each of the 18 regions had a median value of about 33%, although this value varied considerably between particular regional faunas. Species endemism was seen to be largely a function of their biogeographic isolation or proximity to other regional faunas and to ecological factors such as the possession of unique habitat types. Regions with highest levels of relative endemism were Sydney-Illawarra (the most southern region; 81% of species), Wreck Reef (the most isolated oceanic region; 46%), and the Gulf of Carpentaria (differing substantially from all other regions in its habitat composition; 45%). Consistent discovery of about 33% of new (i.e. not previously encountered) species from each reef system surveyed suggests that the possible sponge biodiversity in NE Australia greatly exceeds previous estimates of about 1,500 species.

Within NE Australia (ignoring the S NSW outgroup), five provincial faunas were recognised, grouped hierarchically based on parsimony analysis, each showing greater similarities in species composition within-regions, and fewer similarities between-regions: 1) Tweed River (Byron Bay to the Gold Coast) (with 30% provincial species endemism); 2) SE Qld (Moreton Bay to Hervey Bay) (49%); 3) GBR (Capricorn-Bunker Group to the Cockburn Is) (70%); 4) far northern region (coastal reef and islands in the vicinity of northern Cape York, extending into the Gulf of Carpentaria) (52%); 5) Coral Sea (49%) (although not yet substantially surveyed). Lendenfeld's concept of a homogeneous E Australian coastal fauna is rejected, and the possibility that both the GBR and Coral Sea regions each comprise more than single provinces requires further investigation. □ *Porifera, biodiversity, biogeography, fauna survey, species distribution patterns, endemism, NE Australia, Great Barrier Reef, Coral Sea.*

John N.A. Hooper (email: Johnh@qm.qld.gov.au), Susan E. List-Armitage, John A. Kennedy & Stephen D. Cook, Marine Biology Laboratory, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; Ron Quinn, Queensland Pharmaceutical Research Institute, Griffith University, Corner Don Young Road and Forest Court, Mt Gravatt Research Park, Nathan 4111, Australia; 2 March 1999

This study examines the biodiversity, species composition and biogeographic relationships between regional populations of marine sponges along the NE Australian coastline, extending northwards from the Byron Bay region (N New South Wales (NSW)) to the E Gulf of Carpentaria (N Queensland (Qld)), with the southern fauna of Sydney-Illawarra region used as an outgroup comparison. Our study is based exclusively on our samples of living populations, documented using contemporary methods. For reasons explained below we ignored the published literature completely in these analyses.

Biogeographic relationships of Great Barrier Reef (GBR) sponges in particular, and of the Qld fauna in general, have been speculative ever since the pioneering studies in this region by Ridley (1884), Poléjaeff (1884a,b), Ridley & Dendy (1887), Sollas (1888), Lendenfeld (1883, 1885a,b, 1887, 1888, 1889), Thiele (1898, 1903), Schulz (1900), Kieschnick (1900) and Burton (1934). Together these earlier authors indicated that a large proportion of this fauna consisted of 'widely distributed Indo-Malay', 'Indo-Pacific', 'cosmopolitan' or 'general east Australian coastal' species, with a much smaller proportion of indigenous species.

There is some evidence from contemporary collections to support this contention in the older literature that a certain proportion of tropical and subtropical Indo-Pacific sponges extensively range in distribution from the Red Sea to the central west Pacific islands. These species are thought to comprise between 5% (Hooper & Lévi, 1994) and 15% of regional faunas (Hooper, 1994), and they mostly concern species associated with coral reefs, belonging to many different families and orders (i.e. demonstrating a diversity of reproductive strategies and mechanisms for dispersal). They occupy a diversity of coral reef habitats, including the reef flats and lagoons (e.g. *Hyrtilis erecta* (Keller), *Carteriospongia foliascens* (Pallas)); coral rubble (e.g. *Iotrochota baculifera* Ridley, *Spirastrella* (*Spheciospongia*) *vagubunda* (Ridley), *Tethya robusta* Bowerbank); deeper fringing reefs (e.g. *Axinella carteri* (Dendy), *Ianthella basta* (Pallas)); and specialised habitats such as coral caves (e.g. *Astrosclera willeyana* Lister). The occurrence of these species in a particular region may be linked to the presence or absence of these habitats on each reef (e.g. Hooper, 1994), and in some cases dispersal has been assisted through anthropogenic activities (such as ship bilge water (e.g. *Mycale* (*Zygomycale*) *parishii* (Bower-

bank)), and oyster farming (e.g. *Cliona vastifica* Hancock) (e.g. Wesche et al., 1997)).

Morphometrically these widely dispersed populations appear to be conspecific and in some cases they do not appear to vary morphologically across this vast geographic range. But it is still unknown to what extent these discontinuous regional populations differ genetically, their potential capabilities for interbreeding or re-hybridising, or any realistic estimates of what proportion of these species are truly widely dispersed and what proportion consist of complexes of closely related, but genetically distinct, species (sibling species). Increasingly, however, many of these allegedly widely distributed morphospecies are being found to consist of heterogeneous allopatric populations, with biochemical and genetic diversity not necessarily manifested at the morphological level (e.g. Solé-Cava and Thorpe, 1986, 1994; Hooper et al., 1990, 1992; Solé-Cava et al., 1991, 1992; Bavastrello & Sarà, 1992; Boury-Esnault et al., 1992; Kerr and Kelly-Borges 1994; Kelly-Borges et al. 1994; Klautau et al., 1994; Solé-Cava et al., this volume). To date only one allegedly widely distributed species, *A. willeyana*, has been sampled across the entire Indo-Pacific system, including populations from the GBR (Woerheide, 1997). Chemical and genetic analyses suggest that regional populations of this morphospecies may consist of several discrete sibling species, corresponding to subtle but consistent morphometric differences between them. No other data are yet available for other species from the GBR.

The possibility that regional endemism amongst the GBR and Qld species may be higher than previously recognised (Hooper & Lévi, 1994) is supported from three sources.

1) In the more recent literature on GBR sponges local populations of so-called widely distributed species are recognised as belonging to distinct species (Wilkinson, 1978; Pulitzer-Finali, 1982; Thompson et al., 1987; Hooper, 1987, 1990, 1991, 1996; Bergquist et al., 1988, 1990; Sarà, 1990; Fromont, 1991, 1993; Van Soest et al., 1991, 1996; Hooper & Bergquist, 1992; Van Soest & Hooper, 1994; Bergquist & Kelly-Borges, 1991, 1995; Kelly-Borges & Vacelet, 1995). These contemporary studies differ from the older literature largely through their recognition that consistent (and sometimes subtle) morphometric differences between regional populations may constitute valid interspecific differences, as opposed to merely recognition of (sometimes substantial) intraspecific variability. A common

feature of these contemporary studies is that they were largely based on living populations and not solely reliant on often antiquated, preserved or dry, museum voucher specimens (which lose most of their useful field characteristics). Some of these studies also include chemical and genetic data to support their morphological hypotheses. By comparison, very few authors of the older literature had access to living populations, with few (if any) data on living species' characteristics. For many taxa (particularly Chalinidae, Callyspongiidae, Halichondriidae), such data are mandatory, and consequently, as stated long ago by Hallmann (1912), many of the identifications in the older literature have long been doubtful.

Unfortunately, however, these species described in the contemporary literature comprise only a relatively small proportion of the published fauna of the entire GBR and Qld, with most species names established in the older literature (see Hooper & Wiedenmayer, 1994).

2) Our re-examination of some museum voucher specimens described in the older literature has found many instances where species were misidentified, with regional populations being unjustifiably 'lumped' into a single widely distributed or so-called cosmopolitan taxon (e.g. Hooper, 1991, 1996; Hooper & Weidenmayer, 1994; Hooper et al., 1999, this volume). Unfortunately, again, relatively few of these older species have yet been revised — a long and arduous process — and the status of many nominal species throughout the GBR and Qld faunas is still in doubt. Until identifications can be confirmed, estimates of endemism are equivocal, and endemism is referred to as 'apparent'.

3) Throughout the Indo-Pacific there are published regional faunas which have much higher levels of species endemism and relatively fewer widely distributed species than has been suggested for the GBR and Qld in the older literature. This extra-limital literature includes both earlier authors (e.g. Topsent (1897) and Thiele (1900, 1903) in describing the Ambon and Ternate faunas; de Laubenfels (1954) on the central west Pacific island and atoll faunas) and more contemporary publications (e.g. Bergquist (1968 et seq.) on the New Zealand fauna; Lévi (1967 et seq.) on the New Caledonia fauna). Theoretically, levels of species endemism amongst Qld and GBR faunas might also be expected to approach these other regions, but the existing taxonomic literature is largely unreliable to serve as a basis to analyse faunistic relationships of sponges in this region.

For these reasons, it has not been possible to develop any reliable hypothesis on the biogeographic affinities of the GBR and Qld sponge faunas, even though 428 'valid' species of sponges have already been published from this region (Hooper & Wiedenmayer, 1994; including literature published since 1994). Many of these species are still poorly known, with relatively few subsequently recorded since they were first described (particularly those of Lendenfeld). Moreover, recent collections from this region now consist of >1,500 species, most documented from living populations (Queensland Museum (QM) collections), but most cannot yet be assigned reliably to a known taxon given the largely inadequate descriptions in the older literature, their lack of published data on living characteristics, the significant proportion of misidentifications amongst the so-called widely distributed species, and the inaccessibility, scattered and time-consuming task of locating and re-examining type collections.

Consequently, we chose to make use of these comprehensive, but still largely unnamed QM sponge collections to explore the biogeographic affinities within the Qld regional faunas by ignoring the published literature completely. This literature, concerning the 428 described species from Qld waters, is summarised in Hooper & Wiedenmayer (1994). The QM collections were primarily obtained from shallow coastal waters of the Qld coast, GBR and the Coral Sea (0-70m depth), with accurate GPS locality data, habitat descriptions and underwater photography. They were obtained using SCUBA and trawling, and have been identified and documented to species level (with many already known to be new to science). Our standardised method of collection and documentation provides us with the ability to unequivocally differentiate between closely related sibling species and not to rely solely on the literature to determine conspecificity and faunistics relationships. It is well beyond the scope of this paper to provide a comprehensive list of raw species data used to compare regional and provincial faunas. These raw data have been included (in tabular format) on the senior author's personal web page at the QM web site (<http://www.qmuseum.qld.gov.au>).

Of these QM collections we selected 17 discrete regions within the Qld fauna (i.e. ignoring some of the dispersed inter-reef regions sampled such as the collections described by Cannon et al., 1987). Together these collections consisted of approximately 800 species. As an

TABLE 1. Regional species diversity (bold numbers in the diagonal row) and similarities in species composition between sponge faunas of central and NE Australia (upper half of matrix showing the numbers of species shared between each region; lower half of matrix showing the percentage similarity between regional faunas (Greig-Smith Similarity Index; Krebs, 1978)). Key to regions: A, Sydney-Illawarra region; B, Tweed River region, from Byron Bay to the Gold Coast; C, Moreton Bay region, within the bay and outside the bay from South Stradbroke I. to Flinders Reef, N of Moreton I.; D, Sunshine Coast region, from Mooloolaba to Noosa Heads; E, Hervey Bay region, including W side of Fraser I.; F, N islands of the Capricorn-Bunker Group, S Great Barrier Reef; G, Wreck Reef, S Coral Sea; H, Cato Reef, S Coral Sea; I, Saumarez Reef, S Coral Sea; J, Swain Reefs, S Great Barrier Reef; K, Bait and Hook Reefs, Whitsunday Is region, central Great Barrier Reef; L, Lizard I. region, including the Direction Is and MacGilvray Reef, N Great Barrier Reef; M, Turtle Is region, N Great Barrier Reef (trawled fauna); N, Low Isles, N Great Barrier Reef; O, Osprey Reef, Far N Coral Sea; P, Shelburne Bay region, Far N Great Barrier Reef, including the Cockburn and Fast Is (trawled fauna); Q, Torres Strait region (trawled fauna); R, E Gulf of Carpentaria region (trawled fauna).

Region	Number of shared species																	
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
A	131	10	10	9	2	1	2	0	0	3	2	2	1	1	0	5	1	1
B	10	69	33	14	5	7	1	0	0	8	2	5	4	1	0	6	3	3
C	6.7	28	166	31	18	19	6	1	3	28	8	13	3	7	2	16	4	9
D	7.6	16	23	106	11	19	7	1	1	25	10	23	3	12	6	12	4	5
E	2.2	8.1	16	14	54	11	1	0	0	11	3	7	3	6	3	8	2	4
F	0.6	5.5	11	13	9.1	187	21	5	4	61	22	44	5	25	0	23	5	4
G	1.5	1.3	4.9	7.5	1.5	18	81	7	4	25	7	20	1	12	5	5	6	1
H	0	0	1.1	1.7	0	5	15	14	2	0	1	2	0	2	0	1	0	0
I	0	0	3.4	1.7	0	7	8.6	15	18	4	4	4	0	3	0	2	0	0
J	1.8	5.8	15	16	8.4	31	17	3.6	2.7	208	28	62	0	29	13	27	11	0
K	2.1	3.2	7.2	12	5.4	18	10	2.8	8.7	21	57	31	5	16	4	18	4	4
L	1.3	4.1	7.6	18	6.1	23	18	2.1	3.2	32	27	176	16	39	16	32	12	9
M	1	5.8	2.5	3.4	4.8	3.9	1.3	0	0	4.3	7.9	13	70	0	0	13	0	8
N	0.8	1.1	4.9	11	6.9	16	12	3	4.5	18	18	26	6.3	134	6	22	9	8
O	0	0	2	8.4	6.6	5.4	8.5	0	0	11	8.5	15	0	7.6	37	5	0	1
P	4.3	7.1	12	12	10	16	5.5	1.7	3.5	17	24	23	15	20	7.2	101	16	16
Q	1.1	5.2	3.8	5.3	4	4.3	9.4	0	0	8.7	7.8	11	10	11	0	22	46	9
R	1	4.7	8	6	7	3.2	1.4	0	0	4.5	5.1	7.6	12	8.8	2.1	20	17	60

Similarity Index (%)

outgroup comparison to check on species relationships throughout the Qld faunas we used recent collections of 131 species from the Sydney-Illawarra region, NSW, all of which we have documented, identified and described in the same manner as the Qld voucher material (i.e. again ignoring the published NSW fauna of Lendenfeld (1884 et seq.), Whitelegge (1889 et seq.), Hallmann (1912 et seq.) and others).

MATERIALS AND METHODS

Species diversity, composition and distributions were compared between 17 discrete regional faunas within NE Australia, extending from Byron Bay (N coast of NSW) northwards to the E Gulf of Carpentaria (Qld), including several seamounts in the Coral Sea, and comparing these with the Sydney-Illawarra region (S NSW; see

Fig. 1). From the QM sessile marine invertebrate databases we retrieved 913 species collected from these regions. Some of these species have been described and recorded previously from Qld waters in the literature whereas most cannot be identified with a known taxon (i.e. probably new to science). Only species (known and unknown) for which we have collected a voucher specimen during our contemporary collections were considered in this study. Other species records from the literature from the Qld fauna, for which we do not yet have a voucher specimen in QM collections were ignored and are not included in this study. Hence, the potential diversity of regional sponge faunas is much larger than we consider here, whereas the uncertainty still surrounding some of these taxa preclude us from using them reliably in our species' inventories.

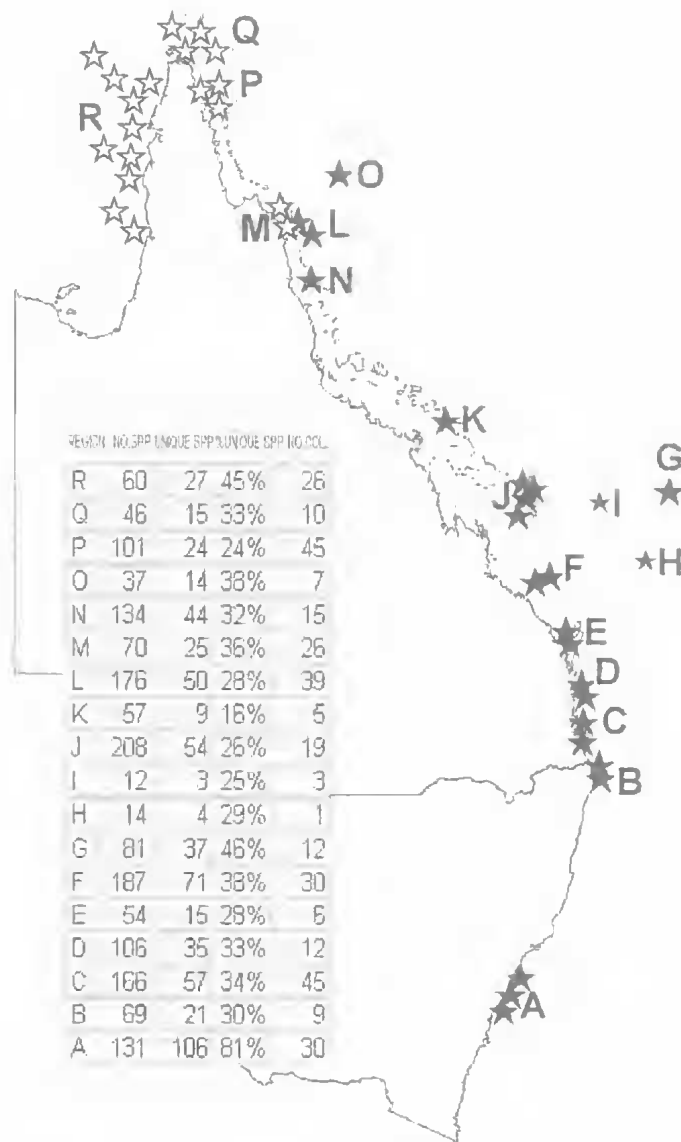


FIG. 1. Distribution of NE Australian regional sponge faunas, showing collecting localities grouped into regional faunas, table of the total number of species collected, the number and percentage of unique species for each region (apparent endemics), and number of collection stations in each region for which sponges were present (see Table 1 for key to regions).

Species lists were generated for each of the regional faunas from the QM databases. Species were then tabulated as present/absent for each of the 18 regions, producing a pairwise matrix of the number of shared species between individual regions, and a simple index of similarity calculated for each pairwise comparison (Greig-Smith 1964, in Krebs, 1978: as $(2 * X / Y + Z)$ where

Y and Z are the total number of species in each region and X is the number of shared species between regions Y and Z, expressed as a percentage). A cluster analysis was performed on all pairwise comparisons and plotted using UPGMA (Group-Average) sorting, and data were checked for consistency using non-parametric Spearman's rank correlation analysis on all pairwise correlations. A hierarchical classification based on a heuristic distance matrix was calculated from all pairwise comparisons using PAUP 3.1.1 (Swofford, 1993) with dendrograms plotted using MacClade (Maddison & Maddison, 1992). Based on these comparisons, regions of highest similarity in species composition were then combined into six provincial faunas and reanalysed using these same methods.

Together these analyses provided information on biodiversity (total number of species within each of the 18 regions); regional endemism (number of unique species within each region); similarities and differences between regional faunas (through a pairwise comparison of similar species for each region, expressed as a total number of shared species and a similarity index), and a biogeographic model (using cluster analysis and distance matrices producing a hierarchical classification of regional faunistics similarities).

RESULTS AND DISCUSSION

SPECIES DIVERSITY. Levels of biodiversity in each of the 18 selected regions (Fig. 1) varied considerably (Table 1), undoubtedly related in part to the size and diversity of habitats present in each reef system. In some cases these differences were biased by differences in the collection effort between regions, whereas in other cases they reflect more true indications of diversity (table in Fig. 1).

TABLE 2. Levels of species endemism for each province (combined regions), showing total number of species, number and percentage of unique species (apparent endemics) in each province (see Table 1 for key to regions).

Region	No. spp	Unique spp	% Unique
A	131	106	81
B	69	21	30
CDE	233	114	49
GHI	95	47	49
FJKLNOP	507	356	70
MQR	142	74	52

Few collections were made at Cato and Saumarez Reefs in the Coral Sea, and these reefs were also relatively homogeneous compared to other regions sampled, both factors reflecting their low sponge diversities (14 and 12 spp. respectively).

In contrast, higher diversities in Moreton Bay (166 spp.), the Capricorn-Bunker Group (187 spp.) and Shelburne Bay (including the Coekburn and Fast Islands) (101 spp.) are undoubtedly related to the presence of larger and more diverse habitats in these regions, although there were also more collections undertaken from each region.

By comparison, Lizard Island and the Low Isles are both relatively small reef systems but contain relatively high sponge diversities (176 and 134 spp., respectively), although the former region had over twice the collection effort of the latter.

The Sunshine Coast (106 spp.) and Swain Reefs (208 spp.) had relatively fewer collections than these other regions but relatively high diversity, the latter the most diverse region yet sampled.

Two inshore faunas, the Turtle Islands (70 spp.) and eastern Gulf of Carpentaria (60 spp.) were characterised by shelly and soft sediments and murky waters, yielding only few species despite relatively higher collection efforts.

These trends are summarised in Figure 4. In the case of Cato Reef, Saumarez Reef, Osprey Reef, Torres Strait and Bait and Hook Reefs, apparent low biodiversity is obviously related directly to collection effort, whereas for other reef systems our collections are more valid indicators of existing sponge diversity. This is particularly evident for Lizard Island, the Capricorn-Bunker Group and the Swain Reefs in which species diversity increased despite a consecutive decrease in collection effort (Fig. 4). These differences are confirmed through one-way ANOVA, comparing

the numbers of species collected, the number of unique species, and the number of collections made (Table 2), showing significant differences between their means ($P < 0.001$).

From our data there is no evidence that species diversity increases at lower latitudes, contrary to some other phyla of marine invertebrates in which biodiversity generally increases towards the equator, especially within the GBR system (e.g. Rohde, 1979). In fact the reverse appears to be true for sponges, in which five of the seven most diverse regions lay in the south (Swain Reefs, Capricorn-Bunker Group, Moreton Bay, Sydney-Illawarra and Sunshine Coast regions), and only two northern regions had comparable sponge diversity (Lizard Island, Low Isles).

SPECIES COMPOSITION. Affinities between regional faunas generally appear to be related to their proximity to each other, such that adjacent regions usually had higher proportions of similar species than did those further apart (Fig. 2). Regions containing the highest proportions of unique species (i.e. apparent endemics) were not necessarily those containing the highest biodiversity; nor were they always artifacts of higher collection efforts ($P < 0.001$; Fig. 4), but were those that were either more isolated or contained substantially different habitats than other regions (table in Fig. 1). The southernmost region, Sydney-Illawarra, had 81% endemic species; the most isolated oceanic coral reef, Wreck Reef, had 46%; and the Gulf of Carpentaria, with mainly soft substrata, had 45% unique species (Fig. 1). By comparison, levels of species endemism for most other regions were consistent (between 24-38%), with the exceptions of Bait and Hook Reefs in the central GBR (16%) which probably contains a more even mixture of species from both northern and southern GBR faunas.

These data support previous contentions that sponge species distributions are notoriously heterogeneous, particularly in coral reef faunas, with differences in faunal composition partly attributed to differences in geomorphology between reefs (Hooper, 1994), but also with biogeographic factors influencing composition (as indicated by the correlation between proximity and similarity in species composition).

For each new reef system visited about 30% of species had not previously been encountered, with many of these possibly also new to science. Thus, our prediction of sponge biodiversity for Qld. (about 1500 species; Hooper & Lévi, 1994; Hooper & Wiedenmayer, 1994), may be a gross

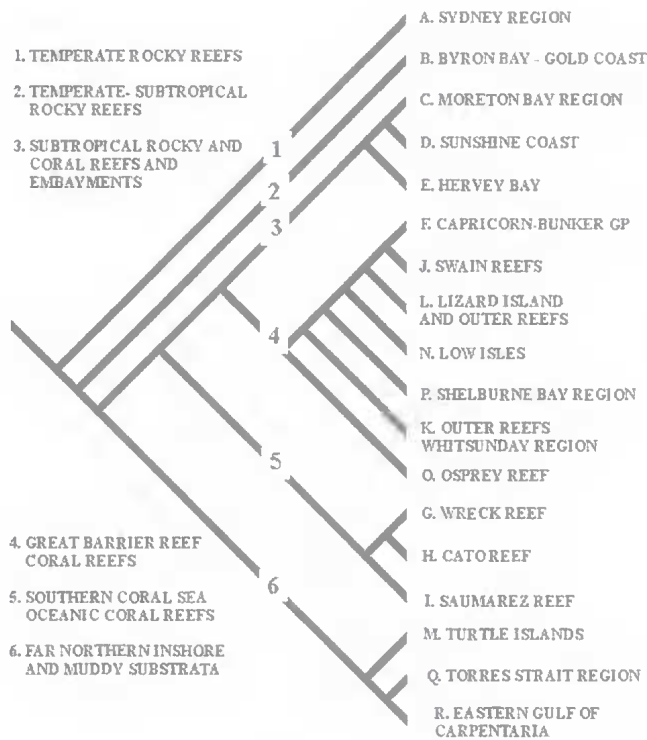


FIG. 2. Cladogram illustrating the hierarchical classification of affinities between regional sponge faunas, based on heuristic distance matrices computed using PAUP 3.1.1, indicating 6 major faunistic provinces. Major provinces are: 1, Temperate rocky reefs; 2, Temperate-subtropical rocky reefs; 3, Subtropical rocky and fringing coral reefs and embayments; 4, Coral islands and reefs of the Great Barrier Reef; 5, S Coral Sea oceanic coral seamounts; 6, Far N coastal islands around Torres Strait and Gulf of Carpentaria, including fringing coral reefs and inter-reef soft substrata.

underestimate, and it is conceivable that twice this number may live in this region.

Parsimony analysis, producing a hierarchical classification of similarities between regions based on regional species compositions (Fig. 2), grouped the 18 regional faunas into 6 logical provinces. These were generally (but not exclusively) correlated with their proximity to each other, their distance from the coast (and terrestrial influences), and possession of similar habitat types in each, such that these provincial groups appear to be valid indicators of biogeographic affinities: 1) Temperate rocky reefs; 2) Temperate-subtropical rocky reefs; 3) Subtropical rocky and fringing coral reefs and embayments; 4) GBR and island coral reefs; 5) Southern Coral Sea oceanic coral reefs; 6) Far northern inshore, fringing coral reefs and inter-reef soft substrata.

REGIONAL BIOGEOGRAPHY.

On the basis of these trends we combined the data for the 18 regional faunas into 6 provincial faunas, and repeated this analysis (Fig. 3, Tables 2-3). Ignoring for the time being the most southern region (Sydney-Illawarra, used as an outgroup comparison), and the most isolated region (oceanic southern Coral Sea), similarities in species composition between the other four provinces along the NE coast ranged from only 18-25%.

Highest species diversity and apparent endemism was found in the GBR provincial fauna (507 spp. and 70%, respectively). It has been suggested, based on more subjective criteria (Hooper et al., 1999, this volume) that recognition of a single GBR fauna may be artificial, with the possible existence of separate northern and southern GBR provinces. To test this we compared the two southern GBR regions (Capricorn-Bunker Group and Swain Reefs), showing a 31% similarity in their species compositions, with the three major northern GBR regions (Low Is, Lizard I. and Cockburn and Fast Is), showing similarities between 20-26%. We then compared the combined data sets for the two southern reefs with those of the three northern reefs, discovering that there

were 88 species in common, with a similarity index of 22%. Thus, between-group comparisons clearly overlap the within-group comparisons, providing no statistical support for a proposal to subdivide the GBR province. Breaking the data down even further and re-examining all the pair-wise comparisons between species similarities for each of the individual GBR regions was also uninformative (Table 1).

Similarly, any biogeographic trends in sponge distributions that may be useful as a basis for subdivision may also be partially masked by the well-known heterogeneity amongst coral reef sponges (Hooper, 1994), with the two factors difficult to separate.

Nevertheless, from present data we can clearly differentiate at least five provincial sponge faunas within NE Australia, each having high levels of within-group regional endemism and

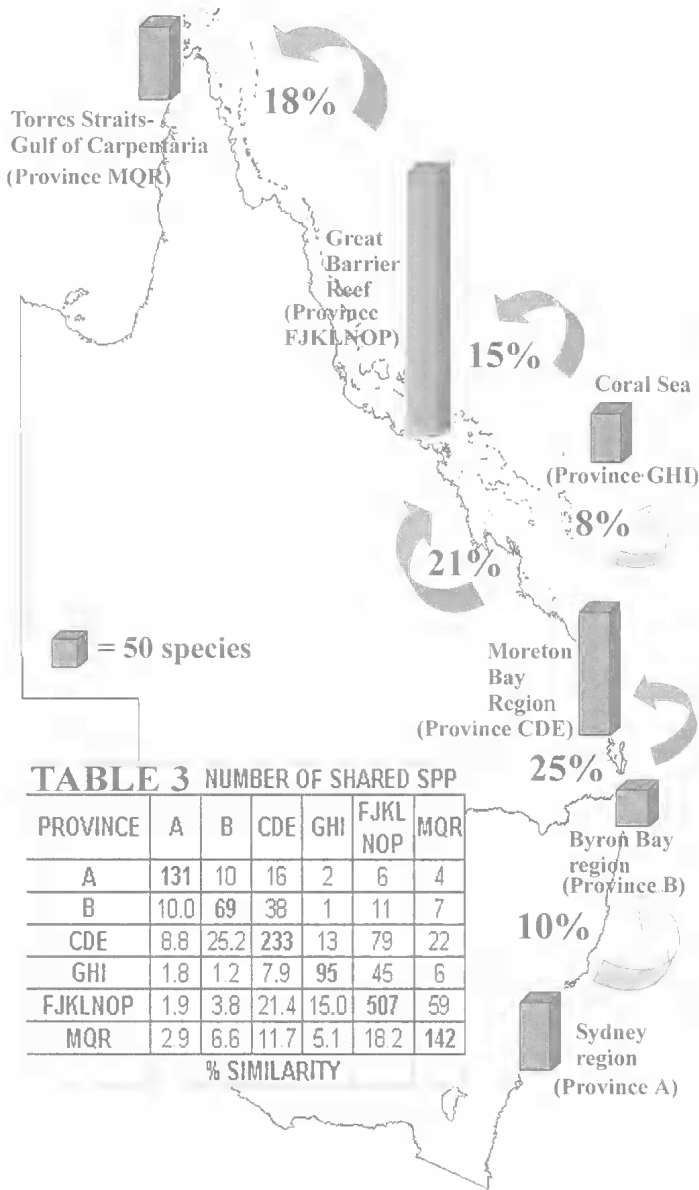


FIG. 3. Distribution of NE Australian provincial sponge faunas (18 regional sponge faunas amalgamated into 6 major provinces based on PAUP analysis), showing species diversity (bar graphs), percentage similarity in species composition between adjacent provincial faunas (arrows) (see Table 1 for key to regions).

TABLE 3. Similarities in species composition between the 6 major provinces (upper half of matrix showing the numbers of species shared between each province; lower half of matrix showing the percentage similarity between provincial faunas using Greig-Smith Similarity Index; Krebs, 1978); and total number of species in each province (bold numbers in the diagonal row) (see Table 1 for key to regions).

relatively low levels of between-group similarities in species composition: 1) Tweed River region (Byron Bay-Gold Coast), with 30% of species not yet found outside this province (apparent endemic species) (Table 2). 2) SE Qld (Moreton Bay-Hervey Bay), with 49% provincial endemism. This fauna is relatively homogeneous in comparison with the other provincial faunas. 3) GBR (Capricorn-Bunker Group - Cockburn Is), with 70% provincial endemism. 4) Far northern coastal and islands region (Torres Strait - E Gulf of Carpentaria), with 52% provincial endemism. It is also likely that this province could be further subdivided, given that the combined Torres Strait - Shelburne Bay regions have only a 17% similarity in their species composition with the Gulf of Carpentaria region (Table 1). 5) Coral Sea, with 49% provincial endemism. Further collections from these seamounts are necessary to determine whether they contain a single homogeneous fauna or several distinct provincial faunas.

The concept of an E Australian coastal sponge fauna, mentioned frequently by Lendenfeld (1888, 1889) is rejected, and the concept of homogeneous GBR and Coral Sea coral reef faunas (cf. Burton, 1934) is also questionable, although more extensive sampling of regional faunas within each of these provinces is required to further investigate any proposed biogeographic subdivisions.

ACKNOWLEDGEMENTS

This project has been funded since 1993 by the Queensland Pharmaceutical Research Institute, Griffith University, Brisbane, and the Queensland Museum, to collect, document and describe marine invertebrate biodiversity throughout NE Australia, and to discover new chemical structures with potential therapeutic pharmaceutical benefits

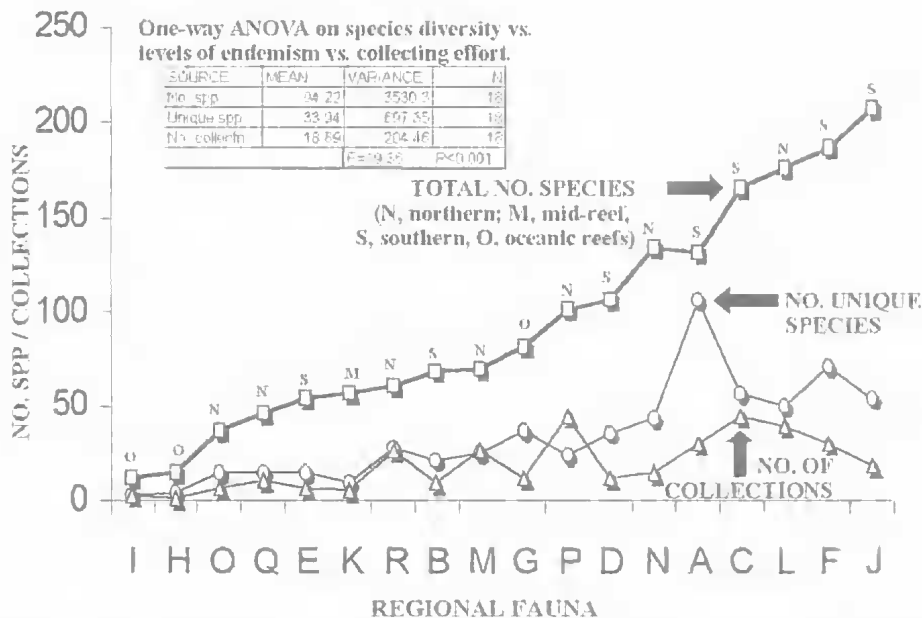


FIG. 4. Comparison between regional species diversity (total number of species collected in each region), endemism (number of unique species in each regional fauna), and collection effort (number of collecting stations in each region that yielded sponges), with regions arbitrarily sorted on increasing species diversity. Results of one-way ANOVA between species diversity, levels of endemism and collecting effort are tabulated.

(‘bioprospecting’). Without the support of Astra Pharmaceuticals (Australia) Pty. Ltd. these extensive collections would not have been possible. For permits to collect throughout Queensland waters and the Coral Sea we thank the Great Barrier Reef Marine Park Authority, Queensland Department of Primary Industries and the Low Isles Preservation Society. For collections of sponges from the New South Wales coast we thank Ms Lisa Miller (AWT EnSight, Pty Ltd), and Mr Danny Roberts (EPA Sydney, now Wyong Shire Council).

LITERATURE CITED

BAVASTRELLO, G. & SARÀ, M. 1992. Morphological and genetic differences in ecologically distinct populations of *Petrosia* (Porifera: Demospongiae). *Biological Journal of the Linnean Society* 47: 49-60.

BERGQUIST, P.R. 1968. The marine fauna of New Zealand: Porifera, Demospongiae, Part 1 (Tetractinomorpha and Lithistida). *Memoirs of the New Zealand Oceanographic Institute* 37: 1-98.

BERGQUIST, P.R., AYLING, A.M. & WILKINSON, C.R. 1988. Foliose Dictyoceratida of the Australian Great Barrier Reef. 1. Taxonomy and phylogenetic relationships. *Marine Ecology* 9(4): 291-320.

BERGQUIST, P.R., CAMBIE, R.C. & KERNAN, M.R. 1990. Scalarane sesterterpenes from *Collospongia auris*, a new thorectid sponge. *Biochemical Systematics and Ecology* 18(5): 349-357.

BERGQUIST, P.R. & KELLY-BORGES, M. 1991. An evaluation of the genus *Tethya* (Porifera: Demospongiae: Hadromerida) with descriptions of new species from the southwest Pacific. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 8(1): 37-72.

1995. Systematics and biogeography of the genus *Ianthella* (Demospongiae: Verongida: Ianthellidae) in the south-west Pacific. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 12: 151-176.

BOURY-ESNAULT, N., SOLÉ-CAVA, A.M. & THORPE, J.P. 1992. Genetic divergence between morphs of the Mediterranean sponge *Oscarella lobularis* Schmidt (Porifera, Demospongiae, Oscarellidae). *Journal of Natural History* 26: 271-284.

BURTON, M. 1934. Sponges. In *Scientific Reports of the Great Barrier Reef Expedition 1928-29*, 4(14): 513-621 (British Museum (Natural History); London).

CANNON, L.R.G., GOEDEN, G.B. & CAMPBELL, P. 1987. Community patterns revealed by trawling in the inter-reef regions of the Great Barrier Reef. *Memoirs of the Queensland Museum* 25(1): 45-70.

- FROMONT, J. 1991. Descriptions of species of the Petrosida (Porifera: Demospongiae) occurring in the tropical waters of the Great Barrier Reef. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 8(1): 73-96.
1993. Descriptions of species of the Haplosclerida (Porifera: Demospongiae) occurring in the tropical waters of the Great Barrier Reef. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 10: 7-40
- HALLMANN, E.F. 1912. Report on the sponges obtained by the F.I.S. 'Endeavour' on the coasts of New South Wales, Victoria, South Australia, Queensland, and Tasmania, 1909-10. Part 1. Zoological Results of the Fisheries Experiments carried out by the F.I.S. 'Endeavour' 1909-10 2: 117-300.
- HOOPER, J.N.A. 1987. New records of *Aearnus* Gray (Porifera: Demospongiae: Poecilosclerida) from Australia, with a synopsis of the genus. Memoirs of the Queensland Museum 25(1): 71-105.
1990. A new species of *Rhabderemia* Topsent (Porifera: Demospongiae) from the Great Barrier Reef. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 7(1): 65-78.
1991. Revision of the Family Raspailiidae (Porifera: Demospongiae), with description of Australian Species. Invertebrate Taxonomy 5(6): 1179-1415.
1994. Coral reef sponges of the Sahul Shelf – a case for habitat preservation. Memoirs of the Queensland Museum 36(1): 93-106.
1996. Revision of Microcionidae (Porifera: Poecilosclerida: Demospongiae), with description of Australian Species. Memoirs of the Queensland Museum 40:1-626.
- HOOPER, J.N.A. & BERGQUIST, P.R. 1992. New species and genus of lamellate coral reef sponges (Demospongiae: Axinellida: Axinellidae). Memoirs of the Queensland Museum 32(1): 99-137.
- HOOPER, J.N.A., CAPON, R.J., KEENAN, C.P. & PARRY, D.L. 1990. Biochemical and morphometric differentiation of two sympatric sibling species of *Clathria* (Porifera: Demospongiae) from northern Australia. Invertebrate Taxonomy 4(1): 123-148.
- HOOPER, J.N.A., CAPON, R.J., KEENAN, C.P., PARRY, D.L. & SMIT, N. 1992. Chemotaxonomy of marine sponges: families Microcionidae, Raspailiidae, and Axinellidae, and their relationships with other families in the orders Poecilosclerida and Axinellida (Porifera: Demospongiae). Invertebrate Taxonomy 6(2): 261-301.
- HOOPER, J.N.A. & LÉVI, C. 1994. Biogeography of Indo-west Pacific sponges: Microcionidae, Raspailiidae, Axinellidae. Pp. 191-212. In Soest, R.W.M. Van, Kempen, T.M.G. van & Braekman, J.-C. (eds) Sponges in Time and Space. (Balkema: Rotterdam).
- HOOPER, J.N.A. & WIEDENMAYER, F. 1994. Porifera. Pp. 1-620. In Wells, A. (ed.) Zoological Catalogue of Australia, Volume 12. (CSIRO Australia: Melbourne).
- HOOPER, J.N.A., LIST-ARMITAGE, S.E., KENNEDY, J.A. COOK, S.D. & VALENTINE, C.A. 1999. Sponges of the Low Isles, Great Barrier Reef: an important scientific site, or a case of mistaken identity? Memoirs of the Queensland Museum (this volume).
- KELLY-BORGES, M., ROBINSON, E.V., GUNASEKERA, S.P., GUNASEKERA, M., GULAVITA, N.K. & POMPONI, S.A. 1994. Species differentiation in the marine sponge genus *Discodermia* (Demospongiae: Lithistida): the utility of ethanol extract profiles as species-specific chemotaxonomic markers. Biochemical Systematics and Ecology 22(4): 353-365.
- KELLY-BORGES, M. & VACELET, J. 1995. A revision of *Diacarnus* Burton and *Negombata* de Laubenfels (Demospongiae: Latrunculiidae) with descriptions of new species from the west central Pacific and Red Sea. Memoirs of the Queensland Museum 38: 477-503.
- KERR, R.G. & KELLY-BORGES, M. 1994. Biochemical and morphological heterogeneity in the Caribbean sponge *Xestospongia muta* (Petrosida: Petrosiidae). Pp. 65-74. In Soest, R.W.M. Van, Kempen, T.M.G. van & Braekman, J.-C. (eds) Sponges in Time and Space. (Balkema: Rotterdam).
- KIESCHNICK, O. 1900. Kieselchwämme von Amboina. In Semon, R. (ed.) Zoologische Forschungsreisen in Australien und dem Malayischen archipel ... ausgeführt in den Jahren 1891-1893. Vol. 5(5). Denkschriften Medizinisch-Naturwissenschaftliche Gesellschaft, Jena 8: 545-582.
- KLAUTAU, M., SOLÉ-CAVA, A.M. & BOROJEVIC, R. 1994. Biochemical systematics of sibling sympatric species of *Clathrina* (Porifera: Calcarea) Biochemical Systematics and Ecology 22(4): 367-375.
- KREBS, C.J. 1978. Ecology. The experimental analysis of distribution and abundance. (Harper & Row: New York, Hagerstown, San Francisco, London).
- LAUBENFELS, M.W. DE 1954. The sponges of the West-Central Pacific. Oregon State Monographs, Zoology 7: 1-306.
- LENDENFELD, R. VON 1883. Über Coelenteraten der Südsee. Neue Aplysinidae. Zeitschrift fuer Wissenschaftliche Zoologie 38: 234-313.
1884. A monograph of the Australian sponges. Part 1. Introduction. Part 2. Morphology and physiology of the sponges. Proceedings of the Linnean Society of New South Wales 9: 121-154, 310-344.

- 1885a. A monograph of the Australian sponges. Part 5. Proceedings of the Linnean Society of New South Wales 10: 282-325.
- 1885b. A monograph of the Australian sponges. Part 6. Proceedings of the Linnean Society of New South Wales 10: 481-553.
1887. Die chalineen des australischen gebietes. Zoologische Jahrbücher, Jena 2: 723-828.
1888. Descriptive Catalogue of the Sponges in the Australian Museum, Sydney. (Taylor & Francis: London).
1889. A Monograph of the Horny Sponges. (Trübner & Co.: London).
- LÉVI, C. 1967. Démonstrations recueillies en Nouvelle-Calédonie par la mission Singer-Polignac. Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie, Fondation Singer-Polignac, Paris 2: 13-28.
- MADDISON, W.P. & MADDISON, D.R. 1992. MacClade. Version 3.0 (Sinauer Associates, Inc. Publishers: Sunderland, Massachusetts).
- POLÉJAEFF, N. 1884a. Report on the Calcareous dredged by H.M.S. 'Challenger' during the years 1873-1876. In Report on the Scientific Results of the Voyage of H.M.S. 'Challenger' during the years 1873-1876. 8(23): 1-76. (Her Majesty's Stationery Office: London, Edinburgh, Dublin).
- 1884b. Report on the Keratosa collected by H.M.S. 'Challenger' during the years 1873-1876. In Report on the Scientific Results of the Voyage of H.M.S. 'Challenger' during the years 1873-1876. 11: 1-88 (Her Majesty's Stationery Office: London, Edinburgh, Dublin).
- PULITZER-FINALI, G. 1982. Some new or little-known sponges from the Great Barrier Reef of Australia. Bolletino dei Musei e degli Istituti Biologici dell'Università di Genova 48-49(1980-1981): 87-141.
- RIDLEY, S.O. 1884. Spongiida. Pp. 366-482, 582-630, pls 39-43, 53-54. In Report on the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of H.M.S. 'Alert' 1881-2. (British Museum (Natural History): London).
- RIDLEY, S.O. & DENDY, A. 1887. Report on the Monaxonida collected by H.M.S. 'Challenger' during the Years 1873-76. In Report on the Scientific Results of the Voyage of H.M.S. 'Challenger' during the Years 1873-76. 20: 1-275 (Her Majesty's Stationery Office: London, Edinburgh, Dublin).
- ROHDE, K. 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. American Naturalist 114: 648-671.
- SARÀ, M. 1990. Australian *Tethya* (Porifera, Demospongiae) from the Great Barrier Reef with description of two new species. Bolletino di Zoologia 57: 153-157.
- SCHULZ, E. 1900. Die Hornschwämme von Thursday Island und Amböina. In Semon, R. (ed.) Zoologische Forschungsreisen in Australien und dem Malayischen Archipel ... ausgeführt in den Jahren 1891-1893. Volume 5(5). Jenaische Denkschriften 8: 525-544.
- SOEST, R.W.M. VAN, HOOPER, J.N.A. & HIEMSTRA, F. 1991. Taxonomy, phylogeny and biogeography of the marine sponge genus *Acarnus* (Porifera: Poecilosclerida). Beaufortia 42(3): 49-88.
- SOEST, R.W.M. VAN & HOOPER, J.N.A. 1994. Taxonomy, phylogeny and biogeography of the marine sponge genus *Rhubderemia* (Porifera: Poecilosclerida). Scientia Marina 57(4): 319-351.
- SOEST, R.W.M. VAN, DESQUEYROUX-FAUNDEZ, R., WRIGHT, A.D. & KOENIG, G.M. 1996. *Cymbastela hooperi* sp.nov. (Halichondrida: Axinellidae) from the Great Barrier Reef, Australia. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 66(Supplement): 103-108.
- SOLÉ-CAVA, A.M. & THORPE, J.P. 1986. Genetic differentiation among morphotypes of the Marine Sponge *Suberites ficus* (Demospongiae: Hadromerida). Marine Biology 93(2): 247-254.
1994. Evolutionary genetics of marine sponges. Pp. 55-64. In Soesi, R.W.M. Van, Kempen, T.M.G. van & Braekman, J.-C. (eds) Sponges in Time and Space. (Balkema: Rotterdam).
- SOLÉ-CAVA, A.M., KLAUTAU, M., BOURY-ESNAULT, N., BOROJEVIC, R. & THORPE, J.P. 1991. Genetic evidence for cryptic speciation in allopatric populations of two cosmopolitan species of the calcareous sponge genus *Clathrina*. Marine Biology 111: 381-386.
- SOLÉ-CAVA, A.M., BOURY-ESNAULT, N., VACELET, J. & THORPE, J.P. 1992. Biochemical genetic divergence and systematics in sponges of the genera *Corticium* and *Oscarella* (Demospongiae: Homoscleromorpha) in the Mediterranean Sea. Marine Biology 113: 299-304.
- SOLLAS, W.J. 1888. Report on the Tetractinellida collected by H.M.S. 'Challenger' during the years 1873-76. In Report on the Scientific Results of the Voyage of H.M.S. 'Challenger' during the years 1873-76. 25(63): 1-458 (Her Majesty's Stationery Office: London, Edinburgh, Dublin).
- SWOFFORD, D.L. 1993. PAUP (Phylogenetic Analysis Using Parsimony). Version 3.1.1 for Apple Macintosh (Smithsonian Institution: Washington).
- THIELE, J. 1898. Studien über pazifische Spongien. I. Zoologica 24: 1-72.
1900. Kieselschwämme von Ternate. I. Abhandlungen der Senkenbergischen Naturforschenden Gesellschaft 25: 19-80.
1903. Kieselschwämme von Ternate. II. Abhandlungen der Senkenbergischen Naturforschenden Gesellschaft 25: 933-968.
- THOMPSON, J.E., MURPHY, P.T., BERGQUIST, P.R. & EVANS, E.A. 1987. Environmentally induced variation in diterpene composition of the marine

- sponge *Rhopaloeides odorabile*. *Biochemical Systematics and Ecology* 15(5): 595-606.
- FOPSENT, E. 1897. Spongiaires de la Baie d'Amboine. Voyage de MM M. Bedot et C. Pictet dans l'Archipel Malais. *Revue Suisse de Zoologie* 4: 421-487.
- WESCHE, S.J., ADLARD, R.D. & HOOPER, J.N.A. 1997. The first incidence of clionid sponges (Porifera) from the Sydney rock oyster *Saccostrea commercialis* (Iredale and Roughley, 1933). *Aquaculture* 157: 173-180.
- WHITELEGGE, T. 1889. List of the marine and freshwater invertebrate fauna of Port Jackson and the neighbourhood. *Journal of the Royal Society of New South Wales* 23(2): 163-323.
- WILKINSON, C.R. 1978. Description of two Demospongiae, one being toxic from the Great Barrier Reef. *Tethys* 8(3): 267-270.
- WOERHEIDE, G. 1997. The reef cave dwelling coralline demosponge *Astrosclera willeyana* Lister 1900 from the Indo-Pacific. (PhD thesis, Universitaat Göttingen: Göttingen).

MORPHOLOGY AND MOLECULES IN LITHISTID TAXONOMY: NEW SOLUTIONS FOR OLD PROBLEMS.

Memoirs of the Queensland Museum 44: 274. 1999:- Most lithistid sponges lack an adequate range of taxonomic characters for differentiation, and in most genera these characters are extremely plastic. Consequently, the generation of morphological hypotheses in comparison with molecular phylogenies is nearly impossible due to the absence of reliable synapomorphies. Historically, lithistids have been grouped together in a single order on the basis of common possession of an interlocking siliceous skeleton. Recent morphological and palaeontological data indicate, however, that lithistid sponges are polyphyletic; several genera possess skeletal characters that suggest affinity with non-lithistid demosponges. We have found that in many cases these characters are probably non-homologous and misleading.

Ongoing research on the phylogeny of lithistid sponges has revealed some interesting 'anomalies' of identification. Although our data collection is still incomplete, we have already found unexpected phylogenetic affinities between three lithistid species in Theonellidae and Corallistidae, comparing morphological and 28S rDNA analyses. Surprisingly, the nearest relatives of de Laubenfel's (1954) '*Plakinalopha mirabilis*' are *Theonella* spp.; *Theonella atlantica* is more closely related to *Corallistes* spp. than to *Theonella* spp.; and *Theonella tubulata* Van Soest is more closely related to *Macandrewia azorica* (in the Corallistidae) than to other *Theonella*.

What is to be done in this situation? To what extent can molecular hypotheses be accepted over morphological hypotheses or vice versa? We have found that rather than having to 'accept' one over the other, which often goes against 'instinctual phylogeny', molecular data makes us re-examine these problems by reciprocal illumination, through the generation of higher quality morphological research and the examination of characters that are often, not at first, obvious. With this group of lithistid sponges, triaene rhabd and clade morphology, microsclere ornamentation, and the patterns of desma zygoses, and shaft ornamentation become crucially important in differentiating taxa.

Thus, for this particular group of organisms, we have found that morphological hypotheses between closely related taxa are often strongly informative and can lend crucial evidence for the acceptance of certain molecular phylogenies over others. Molecular data can clearly indicate relationships between organisms where morphological data had previously failed, and molecular data often require us to re-examine morphological characters from new perspectives, leading the discovery of new taxonomic discriminators. □ *Porifera, phylogeny, 28S rDNA, morphology, congruence, lithistid, Theonellidae, Corallistidae.*

Michelle Kelly* (email: m.kelly@niwa.cri.nz), Grace P. McCormack & James O. McInerney, Zoology Department, Natural History Museum, Cromwell Road, London; * Present address: Marine Ecology and Aquaculture, National Institute of Water & Atmospheric Research (NIWA), Private Bag 109-695, Newmarket, Auckland, New Zealand; 1 June 1998.